8606

Skipjack Population Dynamics; Is It Qualitatively Different from that of Other Tropical Tunas?

DAVID W. K. AU
Southwest Fisheries Center National Marine Fisheries Service, NOAA La Jolla, California 92038, U.S.A.

Some aspects of the population dynamics of skipjack, yellowfin, and bigeye tuna are compared, and an explanation is sought for the large variations in catches of skipjack and the lack of evidence for decline in its populations following fishing. Compared with yellowfin and bigeye, skipjack is an earlier maturing species with higher natural mortality and more variable populations. It follows that its populations have fewer age classes, are more variable from changes in year class strength and availability, and have higher production/biomass ratios. Skipjack may be considered more 'r-selected' than the other tunas, i.e. the species has probably evolved for greater success in the more variable habitats of the tropical ocean through increased potential for population growth. Skipjack therefore should also be expected to be more opportunistic and migratory in comparison to the other tunas. The tropical tunas, but especially skipjack, appear to have specialized in the energy-expensive foraging strategy of sustained, fast-swimming search over large areas, and this is the likely link between their high metabolic and natural mortality rates. It is further suggested that the higher natural mortality of skipjack is more density dependent than in the other tunas, and that this reduces the effects of fishing.

Ce document fait une comparaison de certains aspects de la dynamique des populations du listao, de l'albacore et du thon obèse, et cherche à donner une explication sur les variations importantes des prises de listao et le manque de preuves du déclin de leurs populations par suite de la pêche. Le listao, comparé avec l'albacore et le thon obèse, est une espèce à la maturité plus précoce, à la mortalité plus importante, et dont les populations sont plus variées. En conséquence, ses populations présentent un nombre moindre de classes d'âge, sont plus variables en ce qui concerne les changements de l'abondance et de la disponibilité des classes annuelles, et ont un taux production/biomasse plus élevé. On peut donc considérer le listao plus "r-sélectionné" que les autres thonidés; par exemple, l'espèce a probablement évolué pour mieux s'adapter dans des habitats plus variés de l'océan tropical en augmentant le potentiel de croissance de sa population. On croit donc que le listao est plus opportuniste et migratoire que les autres thonidés. Les thonidés tropicaux, mais surtout le listao, semblent s'être spécialisés dans une technique de recherche de nourriture exigeant de gros efforts, car ils doivent continuellement se déplacer rapidement sur de grandes étendues, et ce phénomène est probablement le lien entre leurs taux élevés de mortalité naturelle et métabolique. Il est également suggéré que la mortalité naturelle élevée du listao dépend plus de la densité que celle d'autres thonidés, ce qui diminue les effets de la pêche.

Se comparan algunos aspectos de la dinámica de poblaciones de rabil, listado y patudo, buscándose explicación a las grandes variaciones en las capturas de listado y la falta de evidencia de descenso de sus poblaciones después de la pesca. En comparación con el rabil y el patudo, el listado es una especie de maduración mas temprana, con una mortalidad natural mas alta y mayor variación en las poblaciones. Por ello, estas poblaciones cuentan con menos clases de edad, la disponiblidad y fuerza de la clase anual experimenta mas cambios y las tasas de producción/biomasa son mas altas. Se puede considerar al listado como una especie mas "r-seleccionada" que el resto de las especies de túnidos, es decir, esta especie ha evolucionado para mejor éxito en los habitats mas variables del océano tropical por medio de un incremento en el potencial de crecimiento de la población. Por lo tanto, se podría esperar que el listado sea mas oportunista y migratorio, en comparación con el resto de los túnidos. Los túnidos tropicales, en especial el listado, parecen haberse especializado en una estrategia para buscar alimento que exige grandes esfuerzos, ya que nadan continuamente por amplias zonas, siendo esta característica el posible lazo de unión entre su rápido metabolismo y sus tasas de mortalidad natural. Se sugiere también, que la alta tasa de mortalidad natural del listado depende mas de la densidad que en el caso de otras especies de túnidos y este hecho reduce los efectos de la pesca.

1. Introduction

Skipjack tuna (*Katsuwonus pelamis*) populations are remarkable in that catches in the various fisheries have risen with little or no indication of declines in stock abundance. Presently total world skipjack catches surpass those of all other tunas, including the two other important tropical species, yellowfin (*Thunnus albacares*) and bigeye tuna (*Thunnus obesus*), whose stocks have shown decline under exploitation. Typically, skipjack abundance, as indexed by catch per unit effort (CPUE), shows large fluctuations but no declining trend with increasing fishing effort. The apparent ability of skipjack to remain unaffected by exploitation prompts the question of whether the species possesses population characteristics different from those of the other tunas. The question is explored in this paper by review of the fisheries and examination and comparison of population dynamics parameters pertinent to these tropical tunas. Particular attention will be paid to natural mortality and how it might be related to, and affected by, the species' foraging methods.

2. Catch and Population Trends

Skipjack catches are second only to those of yellowfin in all the world oceans, except the western Pacific and the Indian Ocean, where its catches rank first (Table 1). The largest catches have come from the western Pacific presently the primary contributor to total world catches, and where over 500,000 mt were taken in 1978 (Table 1). Though the magnitude of skipjack catches suggests large stocks, declines from exploitation are still to be expected.

Table 1. Tropical tuna catches by ocean.[1,2]

Area and Species	1977	1978	1979	1980	1981
1. Atlantic					
East (FAO areas 27, 34, 37, 47)					
Skipjack	90946	90099	78710	93595	89014
Yellowfin	120877	111234	114540	109420	98688
Bigeye	30367	38482	31886	41244	30293
West (FAO areas 21, 31, 41)					
Skipjack	6635	3701	4457	7840	7753
Yellowfin	9866	7234	9715	9555	10012
Bigeye	5574	4881	5820	6309	7692
2. Pacific					
East (FAO areas 67, 77, 87)					
Skipjack	96056	139909	121658	139374	125258
Yellowfin	183610	170460	187630	161330	167324
Bigeye	92039	76449	81511	76291	59207
West (FAO areas 61, 71, 81)					
Skipjack	412974	531013	470034	493743	434168
Yellowfin	177427	187182	188194	211010	214736
Bigeye	51948	41472	44504	45209	37898
3. Indian (FAO areas 51, 57)					
Skipjack	30334	30432	33628	45285	41567
Yellowfin	51748	45270	37566	34851	35585
Bigeye	33722	49074	32039	31968	31867
4. Total Oceans					
Skipjack	636945	795154	537645	779837	697760
Yellowfin	543528	521380	195760	526166	526345
Bigeye	213650	210358	779837	201021	166957

[1] In MT, from FAO (1981)

[2] FAO Statistics are nominal catches and do not include sport-fishing catches. These numbers are generally less than reported in the ICCAT Statistical Bulletins, which include scientists' best estimates.

In reviews of Pacific skipjack fisheries, Forsbergh (1980) and Kearny (1978) found no clear, downward trends in stock size among the various skipjack fisheries. In the long-established eastern Pacific fishery, CPUE statistics, continuous from 1960, indicated no trend in stock abundance (IATTC 1982). Though Pella and Psaropulos (1975) presented evidence for population decrease in the southern area of that fishery after adjusting for increases in fishing efficiency, the effect of exploitation on eastern Pacific skipjack remains uncertain.

Eastern Atlantic skipjack also appear largely unaffected by fishing. Skipjack CPUE indexes from the 1969–1981 surface fishery of France, Ivory Coast, Senegal, and Morocco (Fonteneau et Cayré 1983) showed no evident decline with increasing fishing effort in the expanding fleet of large purse seiners. There was also no suggestion of an upper limit to the catches, though Pianet (1980) had described a parabolic relationship between catch and effort in this fishery. There was some evidence of reduced CPUE at higher effort levels in the pole and line and the medium purse seiner fleets, but in both those fleets there has been a recent trend of decreasing fishing effort.

To compare the variability of skipjack populations to that of the other tunas, the logarithms of eastern Atlantic population indexes for large purse seiner-caught skipjack, yellowfin, and bigeye tuna (Fonteneau et Cayré 1983) were plotted against year (Figure 1). Since the same relative change in successive values shows up as the same change in such plots, regardless of the absolute magnitude of the values, the differences in variability among the species' catch

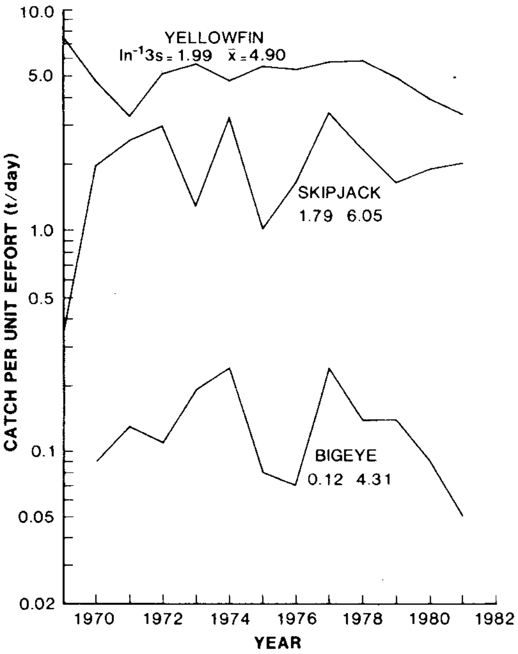

Figure 1. Catch per unit effort on logarithmic scale vs. year for skipjack, yellowfin, and bigeye tunas from the E. Atlantic large purse seiner fleet (Fonteneau et Cayré 1983). Geometric means ($\bar{x}$) and the measure of relative variability ($\ln^{-1} 3s$) are shown for each species.

rates can be compared. The population indexes of skipjack and bigeye are seen to be much more variable than that of yellowfin. Not surprisingly, bigeye tuna catch rates were highly variable, because that species is a secondary target with average catch rate that was only 7% that of skipjack. Bigeye are primarily a subsurface (deep-swimming) species.

The range in relative variability of CPUE, independent of magnitude, may be taken as

$$\ln^{-1}(3s)$$

where $\ln = \log_e$, $\ln^{-1}$ is the antilog, and s is the standard deviation of ln's (CPUE). If CPUE is approximately log-normally distributed, as is to be expected for population sizes, 3s would span about 90% of the observations, and $\ln^{-1} 3s$ would be a measure of the ratio of maximum to minimum CPUE. Values of $\bar{x}$ (geometric mean) and $\ln^{-1}(3s)$ are shown in Figure 1 for the three species of tuna. Skipjack CPUE varied 6.1 × the minumum, while yellowfin had a variability of 2.0 × the minimum. Bigeye tuna had a variability of 4.3 × the minimum.

While the yellowfin catch rates tended to decrease, the skipjack rates in the eastern Atlantic tended to increase after 1976, especially in the skipjack pole and line and medium purse seine fleets (Table 2). If the data indicate five sequential years after 1976 of above average skipjack population size, this would be unusual if the population levels were merely fluctuating randomly about the mean. The probability of a run of at least five sequential, above average years is only $(1-p)p^5 = (.5)(.5)^5 = .016$, or once in sixty-two years. This indicates that skipjack populations, while fluctuating widely, may also be sensitive to external, non-random forces.

Table 2. Tuna catch per unit effort indexes[1] from the eastern Atlantic, pole and line (P/L), medium purse seiner (MS), and large purse seiner (LS) fleets.

	Skipjack			Yellowfin			Bigeye		
Year	P/L[2]	MS	LS	P/L	MS	LS	P/L	MS	LS
1969	0.40	0.84	0.35	1.52	3.78	7.50	0.18	.04	0
1970	0.60	1.31	1.98	1.06	2.35	4.72	0.13	.12	.09
1971	0.93	1.73	2.51	1.20	2.39	3.25	0.10	.07	.13
1972	0.73	1.73	2.95	1.43	2.82	5.10	0.11	.07	.11
1973	0.71	0.92	1.34	1.20	2.48	5.61	0.20	.25	.19
1974	1.00	1.95	3.22	1.39	2.47	4.73	0.13	.11	.24
1975	0.56	1.07	1.02	0.88	2.24	5.47	0.35	.09	.08
1976	0.76	0.83	1.65	1.28	2.01	5.34	0.40	.05	.07
1977	0.99	2.32	3.41	1.25	2.08	5.77	0.92	.16	.24
1978	1.20	2.03	2.34	1.01	1.62	5.81	1.28	.13	.14
1979	1.32	1.84	1.66	0.85	1.65	4.94	0.76	.14	.14
1980	1.40	2.61	1.88	0.99	3.86	3.94	1.06	.01	.09
1981	1.75	3.09	2.00	1.64	2.08	3.37	0.72	.09	.05

[1] Tons per day at sea generated by the fleets of France, Ivory Coast, Senegal, and Morocco (Fonteneau and Cayré 1983).

[2] Primary target of the pole and line fleet is skipjack.

3. Vital Rates and Statistics

In this section, the vital rates of skipjack, yellowfin, and bigeye tunas are compared. Much of the data presented here were first summarized by Yoshida (1979). Instantaneous rates, where given, are expressed on an annual basis.

3.1 GROWTH

Growth in length among fishes is commonly described by the von Bertalanffy growth equation $l_t = L(\infty)(1-e^{-K(t-t_0)})$, (see Ricker 1958: 196). Table 3 summarizes recent values of the growth parameters K and L of skipjack, yellowfin, and bigeye tunas. These parameters are interrelated, but for the purpose of this paper the most important is K, which may be regarded as the rate of development of the growth pattern (Beverton and Holt 1957: 288). K estimates varied approximately from 0.3 to 1.0 for skipjack[1], from 0.3 to 0.5 for yellowfin, and 0.2 to 0.4 for bigeye. Relative to the other tunas, skipjack would seem to develop about twice as fast. This is a tentative conclusion, however, because various methods and different size ranges of fish were used in the derivation of the growth parameters. LeGuen and Sakagawa (1973) and Josse et al. (1979) strongly cautioned against uncritical acceptance and comparison of growth parameters, even when the equations using them are good predictors of observed growth.

3.2 MAXIMUM AGE AND AGE AT FIRST MATURITY

Maximum age has been estimated at 5, 8+, and 9+ years respectively for skipjack, yellowfin, and bigeye by various authors (Table 4 and references). Murphy and Sakagawa (1977) estimated maximum ages of 5, 6, and 7 years for these same species. The table suggests that skipjack have a maximum lifespan perhaps only half that of the other tunas. The age at first reproduction is approximately 1–1.5 years, as opposed to 1.5–3 and 2–3 years for yellowfin and bigeye respectively. Again, skipjack may become mature earlier than the other tunas by a factor of one-half. Since the rate of population increase depends strongly upon how early reproductive maturity is achieved (Cole 1954; Lewontin 1965), there is an increasing trend, from bigeye to skipjack, in the potential for population growth.

---

[1] From Pacific growth rates. In the E. Atlantic Bard and Antoine, (this volume) studied the growth of tagged fish, finding, for $L(\infty)$ set at 80 cm, $K = .332$ in equatorial waters and $K = .601$ in north tropical waters.

Table 3. Parameter estimates of the von Bertalanffy growth equation for skipjack, yellowfin and bigeye tunas.

Species	to	K	$L(\infty)$	Author	Comments
Skipjack	−0.0231	0.5483	102.04	Uchiyama and Struhsaker (1981)	Hawaii, by dialy growth rings
	−0.016	0.432	103.8	Chi and Yang (1973)	W. Pacific; by modal progression
		0.95	85.1	Joseph and Calkins (1969)	Hawaii; by modal progression
		0.431	88.1	Joseph and Calkins (1969)	E. Pacific; tag returns
		0.77	82.3	Rothschild (1967)	C. Pacific; tag returns
		0.94	65.5	Josse et al.	W. Pacific; tag returns
		0.64	79.1	(1979)	E. Pacific; tag returns
		0.52	74.8	Wankowski (1981)	W. Pacific, modal progression
		0.20	79.6	Batts (1972a)	N. Carolina, dorsal spine ''annuli''
		0.32	80	Bard and Antione	E. Atlantic, equatorial; tag returns
		0.60	80	this volume	E. Atlantic, north tropical; tag returns
Yellowfin	−1.032	0.312	197.5, 190	Shomura (1966),	W. Pacific, longline, scale annuli
		0.33	190	*Suzuki (1971),*	
		0.32	188.4	and Le Guen and Sakagawa (1973) resp.	
	0.267	0.454	190.2	Shomura (1966),	Hawaii, mainly longline,
	0.22	0.440	192	Suzuki (1971),	weight frequency
		0.430	191.9	and Le Guen and Sakagawa (1973) resp.	
	0.86	0.60	169	Hennemuth (1961),	E. Pacific, mainly baitboat,
	0.47	0.36	203.3	Le Guen and Sakagawa (1973)	length frequency
	0.83	0.60	.167	Davidoff (1963)	E. Pacific, mainly baitboat length frequency
		0.36	195.2	Yang et al (1969)	W. Pacific, longline, scale annuli
		0.28	222.8	Yang et al (1969)	E. Atlantic, longline, scale annuli
		0.28	223.0	*Le Guen and* Sakagawa (1973)	
	0.52	0.3828	191.7	Le Guen et al. (1969)	E. Atlantic, length frequency
	0.62	0.42	194.8	Le Guen and Sakagawa (1973)	E. Atlantic surface fisheries, length frequency
		0.5568	165.8	Le Guen et	E. Atlantic (Pointe Noire), length frequency
		0.5418	166.5	Champagnat (1968)	
		0.4308	182.3	Le Guen et Champagnat (1968)	E. Atlantic (Dakar), length frequency
Bigeye	0.00055	0.208	215	Yukinawa and Yabuta (1963),	Pacific, scale annuli
	0.017	0.212	213.1	Shomura (1966)	
	0.528	0.38	186.95	Kume and Joseph (1966)	E. Pacific, length frequency
	−1.128	0.16	195.2	Shomura (1966)	Pacific, scale annuli
	−.929	0.27	196.7	Shomura and Keala (1963)	Central Pacific, longline, males, length frequency
	0.718	0.32	183.0	Shomura and Keala (1963)	Central Pacific, longline, males, length frequency

Table 4. Life span and reproductive age estimates for skipjack, yellowfin and bigeye tunas.

	Ages in Fishery:			
Species	Surface	Subsurface (longline)	Max. age	Age at first reproduction
Skipjack	1–3	——	4–5[1]	1–1.5 years[2]
Yellowfin	1–5[3]	2–6+[4]	8+[5]	1.5–3 years[6]
Bigeye	1–4[7]	2–7+[8]	9+[9]	2–3 years[10]

[1] Approximate age of 850 mm fish (see Shomura (1966))

[2] 400–450 mm fish; growth curves of Uchiyama and Struhsaker (1981), Joseph and Calkins (1969)

[3] Honma and Suzuki (1978), Cole (1980), Hayasi and Honma (1971)

[4] Shingu et al. (1974), Hayasi and Honma (1971), Honma et al. (1971)

[5] Hayasi and Honma (1971)

[6] Kikawa (1962), Orange (1961), Ueyanagi (1966), Yuen and June (1957)

[7] Kume and Joseph (1966)

[8] Sakamoto (1967), Kume (1967)

[9] Sakamoto (1967)

[10] Calkins (1980), Kume and Joseph (1966), Kikawa (1962), Kume (1967)

3.3 NATURAL MORTALITY

Natural mortality rate perhaps gives the most insight into the population dynamics of species. It is also the most difficult parameter to estimate. Most measures of the instantaneous natural mortality rate, M, for tunas have been obtained from studies of yellowfin (Table 5). Indeed the value of 0.8 for yellowfin by Hennemuth (1961) is something of a standard in tuna population dynamics, even though his sample was from the pole and line fleet, where larger (older) individuals were probably under-represented. Studies of primarily long-line caught yellowfin, where emigration was considered, have suggested lower rates (Honma et al. 1971, Ishii 1969, Hayasi and Honma 1971). A population model by Francis (1977) of the eastern Pacific surface yellowfin fishery had better correspondence to observed dynamics when M was set at 0.6. There are only a few estimates of M for bigeye tuna. They range from 0.35 to 0.68, and are similar to those of yellowfin (Table 5).

There are also few estimates of skipjack natural mortality, and a value of 0.8, as in yellowfin, is often assumed. Murphy and Sakagawa (1977) considered skipjack M to be between 0.69 and 0.93, on the basis of the relationship between M and the growth constant K (Table 5). The difficulty with this and similar correlations is that the variables may already be correlated through the estimates of age. This is because, as Beverton and Holt (1959) noted, age span in fishes appears adjusted to the time needed to complete the growth pattern.

Although natural mortality must be inversely related to age span, there is no simple way of deriving M from estimates of maximum age (t_{max}). In the presence of mortality there is not a simple relationship between maximum age and mean age; it is the latter that is actually inversely related to M. Mean age is not a firm statistic, especially for skipjack. If natural

Table 5. Estimates of instantaneous natural mortality (M) for skipjack, yellowfin and bigeye tunas.

Species	M/year	Author	Comments
Skipjack	3.00	Bayliff (1977)	tagging data; uncertain reliability
	1.68	Joseph and Calkins (1969)	tagging data; uncertain reliability; emigration, etc. losses included
	0.69–0.93	Murphy and Sakagawa (1977)	from relationship between M and K (of von Bertalanffy equation)
Yellowfin	0.64–.80–.92	Hennemuth (1961)	E. Pacific 1955–59, primarily baitboats
	0.55–1.05	Schaefer (1967)	Revision of Hennemuth (1961)
	1.2	Honma et al. (1971)	C. and W. Pacific; high values (1971) suggested as possibly due to emigration at ages 3.5+
	0.44	Ishii (1969)	Pacific; all-age average; emigration accounted for
	0.3–0.8	Hayasi and Honma (1971)	Summary of several Japanese studies
	0.35–0.44	Kawakami and Kitahara (in Suda 1971)	Indian Ocean
	0.60	Francis (1977)	From model simulating E. Pacific surface fishery
Bigeye	0.35–0.56	Ishii (1968)	Pacific; simulation model of fishery
	0.36	Suda and Kume (1967)	Pacific; age 6 and longline caught fish
	0.44–0.68	Murphy and Sakagawa (1977)	Relationship between M and K (of von Bertalanffy equation)

mortality of the exponential type were acting alone upon an adult population, where youngest age was t_a, we could obtain M as:

$$M = 1/(\bar{t}-t_a)$$

where $\bar{t}$ = average age. The average age should fall between t_a and $(t_{max}-t_a)/2$ (the latter e.g. in the unlikely case that mortality was zero in the interval). If t_a were set at 1 year and t_{max} at 5, 8, and 9 years (see above) for skipjack, yellowfin, and bigeye respectively, the range for $\bar{t}$ would be 1–2, 1–3.5, 1–4.0 years respectively. Even within this restricted range, the possible values of $\bar{t}$ lead to sets of calculated M too imprecise to be useful.

The idea that M is constant throughout the adult life of fish is largely an assumption, but consistent with the observation that animals without notable learning, and subject mainly to random accidents or predation, tend to die at a constant rate. Bird survivorship curves are the classic examples of this pattern. However, in a review of survivorship among various vertebrates, invertebrates, and plants, Hutchinson (1979) found a variety of mortality patterns, depending less upon classification than upon the relative vulnerabilities of juvenile, adult, and senile stages, and the abruptness of the transition between the stages. In this regard one should note that fish, unlike birds, grow to many times over their initial adult weight, skipjack over four times and yellowfin and bigeye over ten times between ages 1 and 2 years. Finally, an age constant M might not be expected if natural mortality in tropical tunas is due to the cost of obtaining sufficient food rather than directly to predation.

3.4 M AND METABOLIC RATE

The apparent high natural mortality rate of tropical tunas may be puzzling, considering the relatively large size and great locomotory power of these fish. An M of 0.8 that is often assigned to yellowfin is in the upper range of natural mortality among commercial species that grow > 50 cm (e.g. Beverton and Holt 1959). It seems likely, though, that the high natural mortality of tunas is associated with their high metabolic rates.

The metabolic, digestive, and respiratory rates of tropical tunas may be the highest among all teleosts (Magnuson 1978, Stevens 1972, Gooding et al. 1981). Kitchell et al. (1978) explained how physiological limits to the ability to process food, together with high metabolism, could result in increasingly reduced energy for growth in larger skipjack. One would therefore expect increasing natural mortality rate among older fish. Comparing survivorship, one notes that unlike skipjack, yellowfin and bigeye survive to form fishable populations of older fish at deeper and cooler depths. Their retention of the gas bladder into adulthood, adaptive if feeding excursions from depths to the surface are no longer frequent, and their lower natural mortality indicate an adaptive departure from the skipjack condition (Sharp 1978).

The general relationship that smaller, shorter-lived (higher M) species have higher metabolic and population increase rates, while larger species show the opposite tendency (Bonner 1965; Fenchel 1974) is consistent with the correlation of M and higher metabolism. Bourliére (1957) reviewed experiments performed on both vertebrates and invertebrates and concluded there was a negative relationship among and within species between metabolic rate and lifespan. Evidence that reproductive activity decreases adult survival and growth while increasing energy expenditure in fish and other animals was summarized by Stearns (1976). Priede (1977) described a model relating increased natural mortality to increased time spent in high energy activity. The link between metabolic rate and M is further supported by the significant correlation between M and water temperature in fishes (Pauley 1980). His compilation of evidence showed that for fish growing > 50 cm, M > 0.8 is often reported among tropical species.

3.5 METABOLISM AND FORAGING STRATEGY

It seems that a high metabolic rate developed in the tropical tunas to meet the requirements of an energy-expensive foraging strategy. The external morphology and behavior of these tunas suggests that this strategy is sustained, fast-swimming search for sparsely distributed food over large areas. The development of this ability doubtlessly played an important role in making it possible for these tunas to expand into the relatively unproductive, offshore tropical ocean. The selective pressure involved can be appreciated by considering the probability P(x) of encountering food items or patches by random searching in a horizontal plane. In search theory (Koopman 1956), the distance x required to achieve a certain cumulative probability P(x) of encountering a randomly distributed target is

$$x = \frac{-\ln[\,1-P(x)]}{k}$$

where k is the instantaneous probability of detection in a small distance interval dx. Since the numerator is a constant for a given P(x), any reduction in k, e.g. due to lowered average density of food, requires a disproportionate increase in search distance x (and energy expenditure) according to a hyperbolic relationship, the effect being stronger for larger P(x) (Figure 2). The short-lived skipjack are apparently faster and more far-ranging than the other tropical tunas (Kearney 1978), indicates a strong specialization in this direction. Their abundance, even in the relatively unproductive, deep-mixed layers of the central and western tropical oceans (Forsbergh 1980; Kearney 1978), indicates the species' success. However, the cost of this specialization seems to be natural mortality more severe than in the other tropical tunas.

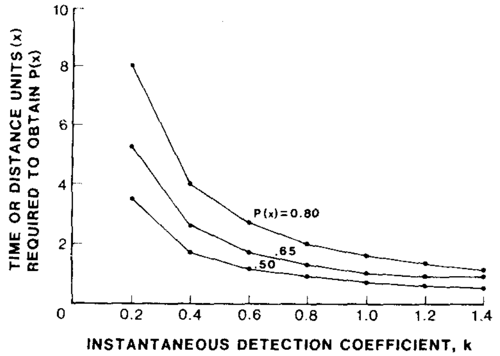

Figure 2. Hypothetical example illustrating the change in time or distance required for successful search (i.e., obtaining P(x) in some unit of time) as a function of the instantaneous detection probability or coefficient, k. P(x) is the cumulative probability of intercepting food after x time or distance units. k can be considered a measure of the average density of food in the environment being randomly searched. See text.

3.6 Production and Critical Age

The leading role of tunas in tropical ocean fisheries is due to their high productivity and large habitat, roughly the entire tropical and subtropical ocean. These fish are productive not in spite of their high natural mortality, but as a correlate to it. Allen (1971) showed that for exponential mortality and von Bertalanffy growth (as well as several other growth models), the production/biomass ratio over a cohort's life is equal to its (constant) mortality rate. Over shorter periods, during which growth may be considered exponential, this ratio is equal to the instantaneous growth rate. From Table 5 estimates of M for skipjack, yellowfin, yellowfin and bigeye might be e.g. 1.0, 0.7, and 0.5 respectively, so that the production/biomass ratio of skipjack could be 43% and 67% larger, respectively, than that of yellowfin and bigeye tuna.

It is useful, too, to look at the instantaneous growth rate, $g = \log(w_{t+1}/w_t)$, relative to M, to determine the critical age or size of individuals in a cohort, i.e. when $g = M$ and the cohort's biomass is largest. Figure 3 shows that the weight specific or instantaneous growth rate is less at a given age for the smaller skipjack in comparison to yellowfin and bigeye, and that the critical age is 1–1.5 years for skipjack, about 2 years for yellowfin, and 2.5–3 years for bigeye. The yield per recruit (Y/R) consideration of fishery population dynamics seeks to determine the harvest at the critical age, but under a practical exploitation schedule over several ages. With few significant age classes in skipjack populations, and the low critical age, it is clear that increases in Y/R of this fish would accrue mostly from increasing fishing mortality, not from increasing age at entry to the fishery.

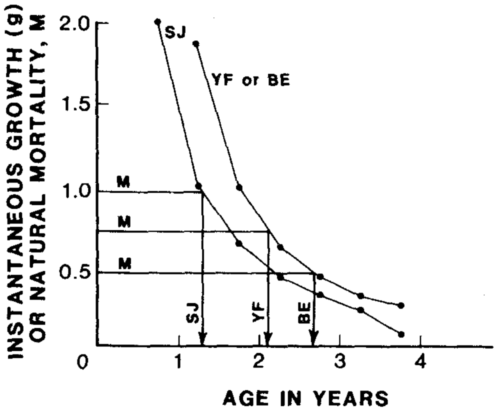

Figure 3. Instantaneous growth rate, g, vs. age as calculated for skipjack, yellowfin, and bigeye. Critical age is indicated by arrows, defining condition where g = natural mortality, M. Growth equations are by Joseph and Calkins (1969) and Hennemuth (1959b) for skipjack, Chatwin (1959) and Le Guen and Sakagawa (1973) for yellowfin, and Kume and Joseph (1966) and Morita (1973) for bigeye.

4. Discussion

This review of skipjack population characteristics indicates that the species may develop about twice as fast and mature twice as early as yellowfin and bigeye. Its natural mortality may be near 1.0 yr^{-1}, which would make its production/biomass ratio perhaps 43% greater than that of yellowfin. In these respects skipjack are "r-selected" relative to yellowfin and bigeye. This term does not strictly refer to the parameter r but rather to a type of survival strategy (see Southwood et al. 1974). As such, skipjack should be more opportunistic, productive, and migratory, and more affected by environmental changes. The species seems qualitatively different in this context.

Skipjack are notable in being composed of only two or three significant age classes that support surface fisheries only. This simple population structure can exacerbate effects of fluctuations in year-class strength. If R is the average annual recruitment, the average fraction of a stock at equilibrium comprised of first year fish is $[R(1-e^{-M})/M]/[R/M] = 1-e^{-M}$ (Ricker 1958: 28). If $M = 1.0$, on average 63% of the stock will be of the incoming year class. Therefore, abundance indexes will be strongly affected by year class fluctuations and, until recruitment is affected, it may be difficult to see the effects of fishing. The extensive movements of the species must also contribute to fluctuations in availability to the fishery, and this too will make analysis of population structure difficult. The range of fish size available to the fishery at any particular time seems especially variable in skipjack, giving length-frequency modes that are erratic and short-lived. This is the basic reason why it is difficult to measure mortality rates in this species.

An interesting hypothesis from modern population theory is that species with intrinsic rates of increase greater than 2.0 year^{-1} can be induced to exhibit stable, or even "chaotic," fluctuations of population size, basically because of strong overcompensation of population response to changes in density (May et al. 1974; May 1976). While the intrinsic rate of increase, r, for skipjack cannot be estimated with confidence because of poor understanding of net reproductive rate and mean generation length, one can note that r is probably much less than 2.0. Even if it were twice that of the Pacific sardine, whose r was estimated as 0.34 by Murphy (1967), the intrinsic rate of increase of skipjack, and probably most commercial fish, would be far below 2.0. This is the reason why even productive fish species can be fished down to levels where recovery is impaired. In contrast, many other animals, e.g. small rodents with mean generation lengths less than one year, have r's greater than 2.0 (Caughley 1977: 112), and their recovery from "overfishing" is virtually assured, and a recurring problem. One must conclude, therefore, that population fluctuations of skipjack are primarily direct responses to external perturbations affecting survival, rather than to sustained oscillations.

An erratic population size and yield will induce a fishery to focus on short-term exploitative goals that are also consistent with recommendations that would come from standard population analyses. Provided that fishing does not impair reproductive potential, skipjack fishing should be as intense as practical.

Most features of skipjack populations appear to be consistent with what might be predicted from the comparison of population dynamics parameters among the three important tropical tunas. However, the comparison did not lead to an explanation of why skipjack appear so unaffected by exploitation. The question remains of how a population, such as that of the eastern Atlantic skipjack, can continue to support catches of over 100,000 mt per year and not show clear evidence of decline. There are at least two possibilities:

1) There is a decline, but it is not detectable in the overall CPUE statistics because of large variability in the resource or its availability or because of changes in fishing efficiency. Skipjack populations may be so variable that underlying population trends cannot yet be detected, or so productive and widespread, relative to the fisheries, that the latter have local effects only, i.e. the fisheries have not yet subjected entire stocks to significant exploitation. This argument may be applicable to eastern and western Pacific skipjack resources, but is less credible in the Atlantic, where the major fishery is in the Gulf of Guinea and the stock presumably smaller, but still without clear evidence of decline. With respect to increased fishing efficiency, the catchability (q) of schools from reduced populations could have increased so as to mask the evidence for decline. However, this seems unlikely to be an important factor in skipjack, considering the species' extensive habitat and high mobility.

2) The high natural mortality of skipjack may actually decrease under exploitation. First, skipjack must compete to some extent with yellowfin and bigeye tunas so that reductions in the latter tunas may be beneficial. If skipjack are the more opportunistic, i.e. "r-selected," of these tunas, it would be the species most likely to respond positively when simultaneous reductions in population size of these fishes occur. Second, and I think more likely, skipjack natural mortality may actually decrease under exploitation from intraspecific, density dependent effects that are a function of the foraging behavior. The probability of not encountering adequate food may increase in large schools that may be more common in lightly exploited stocks. Fish so disadvantaged may weaken rapidly, swim less strongly, and suffer further reduction in their food encounter rate. Similar difficulties are faced by certain stream dwelling fishes that must swim into the current, holding position there in order to ensure adequate food. Juvenile salmonids, for example, obtain their drifting food by maintaining position in preferred locations, either directly in the current or in the eddies, depending upon stream velocity (Symons 1976). Those fish unable to station themselves in positions of adequate food-flow become weaker, fall behind to less advantageous sites, and suffer a higher mortality that is density dependent (Au 1972).

The important feature of density dependent natural mortality is that fishing mortality can compete with it, rather than simply add to it. As a result, total mortality (natural + fishing) could change little as fishing effort is increased. For example, the total mortality rates (Z) of exploited eastern Pacific skipjack have apparently not increased with increasing fishing effort (Table 10 in IATTC 1982). Kearney (1978) proposed that skipjack were subject to large fluctuations in natural mortality to explain the large annual fluctuations in catches from the western Pacific. I suggest that changes in natural mortality may be density dependent and that this feature is more strongly developed both in developmental stages and in species that have high natural mortality.

Density dependent, high mortality is a feature of the larval and juvenile stages of many fish. It probably is the mechanism whereby many marine fishes exhibit no trend in average numbers of recruits over wide ranges of population size (Harris 1975; Beverton and Holt 1957: 51). The above hypothesis on adult skipjack natural mortality is not supported by data, but if correct, then skipjack may be considered a tuna that, with respect to natural mortality, has largely remained at the juvenile stage.

This paper has emphasized the importance of natural mortality as an indicator of a number of aspects of population biology. Unfortunately we know little about this mortality and estimates of its value are imprecise. Studies focused on individual fish could contribute much to understanding how natural mortality is affected by age and population density. Learning about the condition or fatness of tunas of different sizes, from different areas, from schools of different sizes, and from different locations within a school, would help test and develop hypotheses about mortality.

Acknowledgements

I thank N. Bartoo, P. Kleiber, and G. Sakagawa for help in writing the original version of this essay. I am especially grateful for subsequent, detailed help from J. Wankowski.